Title: Cranial Anatomy of the Desert Dormouse, *Selevinia betpakdalaensis* (Rodentia, Gliridae), revealed by Micro-Computed Tomography

Authors: Jesse J. Hennekam[1], James W.F. Sadler[1], Fedor N. Golenishchev[2], Lyudmila Yu. Kryuchkova[3], Dmitry Korost[4], Olga Nanova[5], Philip G. Cox[1,6]

Affiliations:

[1]*Hull York Medical School, University of York, United Kingdom*

[2]*Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia*

[3]*Saint Petersburg State University, St. Petersburg, Russia*

[4]*Department of Geology and Geochemistry of Fossil Fuels, Geological Faculty, M.V. Lomonosov Moscow State University, Moscow, Russia*

[5]*Zoological Museum, M.V. Lomonosov Moscow State University, Moscow, Russia*

[6]*Department of Archaeology, University of York, United Kingdom*

Corresponding author: Jesse J. Hennekam

Address: PalaeoHub, University of York, Wentworth Way, York, YO10 5DD, UK

Email: jjh556@york.ac.uk

Abstract

The dormice (Gliridae) represent a relatively small family of rodents, but exhibit considerable variation in their cranial anatomy. The skull morphology of almost all genera of dormice was described from osteological specimens by Wahlert et al. (1993). However, the rare desert dormouse, *Selevinia betpakdalaensis*, was only assessed using previous descriptions and photographic images, resulting in difficulties with assigning all cranial features within this particular genus. In this study, the crania and mandibles of two adult individuals of this genus were scanned using micro-computed tomography and virtually reconstructed. From these reconstructions, we describe in detail the highly unusual cranial and mandibular morphology of the desert dormouse and determine the states of the cranial and mandibular characters described by Wahlert et al. (1993). These morphological characters were used to compare this species with previously described dormouse genera, showing a clear resemblance between *Selevinia* and the small mouse-tailed dormouse genus *Myomimus.* Derived morphological features unique to *Selevinia* indicate clear adaptations to a desert-like environment, as well as hinting towards an insectivorous diet and burrowing lifestyle.

Introduction

The first description of the desert dormouse *Selevinia betpakdalaensis* dates back to 1939 by Belosludov and Bashanov, based on specimens collected in 1938 by B. A. Belosludov and V. A. Selevin (Bashanov and Belosludov, 1941). Initially placed in Muridae based on its dental formula, further analyses led to the first description of this species published in English (Bashanov and Belosludov, 1941), in which it was placed in a new monospecific family, Seleviniidae. These authors mentioned the close resemblance of the skull morphology of this species with that of members of Gliridae (Myoxidae), but highlighted the atypical dental

structures within this species in comparison to dormice. Ognev (1947) identified the animal as a highly derived dormouse and emphasised the resemblance of this species to *Myomimus.* He therefore created the subfamily Seleviniinae within the family Gliridae. More recent analyses of the enamel structure in this animal and other dormice also incorporated *Selevinia* within Gliridae, and no longer acknowledged Seleviniidae as a sister group of Gliridae (von Koenigswald, 1992). Storch (1994) assigned *Myomimus* and *Chaetocauda* to Seleviniinae alongside *Selevinia*, regarding it as the most primitive of all extant dormice subfamilies. In contrast, Yachontov and Potapova (1991) considered *Selevinia* to be more closely related to *Muscardinus* and *Glis*, belonging to the subfamily Glirinae. Later, Potapova reasserted the close relationship between *Myomimus* and *Selevinia* based on middle ear morphology (Potapova, 2001). Wahlert et al. (1993) placed *Selevinia* and *Myomimus* in the tribe Seleviniini, which, joined with the tribe Leithiini, formed the subfamily Leithiinae. Due to the scarcity of accessible specimens, *Selevinia* was not included in the phylogenetic analyses of the Gliridae based on molecular data by Montgelard et al. (2003) or Nunome et al. (2007). The exact placement of the species within the dormouse phylogeny therefore remains unclear. However, the current consensus is to place the monospecific genus within the subfamily Leithiinae and refrain from the use of Seleviniinae (Holden-Musser et al. 2016).

Eighty years after its first description in the literature, a great deal is still unknown about the desert dormouse. The inhospitable desert environment in which it lives has resulted in only a few specimens being captured in the wild. We know of five specimens of the species caught by hand during an expedition in 1938, and another specimen in 1946. The species appears to be widely distributed in the south and east parts of Kazakhstan, especially in the deserts surrounding Lake Balkhash, and has been documented as far south in Kara-Ungur, near the

border with Kyrgyzstan (Bashanov and Belosludov, 1941; Holden, 2005). The animal is likely predated on by birds of prey, as *Selevinia* material has been reportedly found in bird pellets (Argyropulo and Vinogradov, 1939). Bashanov and Belosludov (1941) noted that the coat of the animal is quite long and dense. It is light grey in colour dorsally, including some dark specks, but light grey and slightly yellowish ventrally. The ears are rather large, including reddish hairs on the outside. No clear facial mask, as seen in *Eliomys* for example, is apparent. The tail is short haired and dark grey dorsally, but significantly lighter ventrally. The forepaw includes four digits, and the hind leg has five, with the soles lacking in hair. The five specimens analysed by Bashanov and Belosludov (1941) showed a total body length varying between 78 and 95 mm, with the tail length varying between 58 and 77 mm. Cranial length was only assessed in three specimens, indicating a range between 21.5 and 22.1 mm.

Wahlert et al. (1993) described the cranial morphology of most extant dormouse genera using a total of 54 cranial and mandibular characteristics. At the time, the authors did not have access to cranial material of *Selevinia*, but instead used former descriptions and dated photographic material to assess the morphological characteristics within the genus (Bashanov and Belosludov, 1941; Ognev, 1947). Due to the resolution and orientation of the figures consulted, the states of many cranial characters could not be reliably determined in the genus. Here, we use microCT data of two adult specimens of *Selevinia betpakdalaensis* in order to describe the cranial anatomy of this species and to complement the dataset created by Wahlert et al. (1993). We believe this to be the first time this species has been scanned using microCT, allowing us to assess the cranial morphology of this species in very high detail. This description will result in a much greater understanding of the distinct morphological features present in

the desert dormouse, and will enable us to compare this species with other dormouse taxa more accurately.

Materials and methods

The sample comprised the skulls and mandibles of two adult specimens of the species *Selevinia betpakdalaensis*, both housed in Russian institutions. Specimen ZIN 32206 is an adult male collected on the 21st August, 1946, by M. A. Musarov near the Meteo Station in Betpak-Dala Desert (46°02'N; 70°12'E). It was placed in the Zoological Institute of Kazakh Academy of Sciences with the incoming number 34-1947. The specimen was later transferred to the Zoological Institute in Saint Petersburg on the 27th May, 1947. The material, consisting of an intact skull and a slightly broken mandible, was scanned at the Research Centre for X-ray Diffraction Studies of Saint Petersburg State University (Saint Petersburg, Russia), using a high-resolution X-ray computed micro-tomography scanner (SkyScan 1172) with an isometric voxel dimensions of 4.9 µm. The specimen was later downsampled to 9.8 µm in order to decrease the computation time whilst rendering the object for analysis. Dentition was analysed using the original 4.9 µm resolution.

Specimen S-28487 was captured in the northern part of Betpak-Dala Desert by V. Selevin on 8th August 1938. The specimen is considered a paratype and was donated to the Zoological Museum in Moscow. The external morphology of this specimen is shown in Fig. 1. A microCT scan of the skull and two hemi-mandibles was created at the Geology department of Moscow State University (Moscow, Russia) on a SkyScan 1172. The resolution of the scanned material is 15.42 µm.

Three-dimensional virtual reconstructions of the skull and lower jaw of each specimen were created from the microCT scans using the segmentation function of Avizo 9.2 (Thermo Fisher Scientific, Waltham, MA, USA). Both surface files of the scanned dormice were uploaded to the online database Morphosource (www.morphosource.org). Linear measurements of the cranium and dentition were recorded from the reconstructions and are given in ESM 1. The virtual reconstructions were used to produce detailed descriptions of the cranial, mandibular and dental anatomy of *Selevinia betpakdalaensis*, and to determine the character states of the 54 anatomical characters used by Wahlert et al. (1993) in their analysis of dormouse cranial anatomy (ESM 2). The morphology was also compared to all other dormouse genera, but in particular *Myomimus* and *Muscardinus*, because the former has been hypothesised to have a close phylogenetic relationship with *Selevinia* (Wahlert et al., 1993; Storch, 1994; Potapova, 2001) and the latter is a similarly small-sized dormouse. The character state data for *Selevinia* were combined with data for all other dormouse genera (except *Chaetocauda*) and four outgroup taxa (*Paramys*, *Sciurus*, *Sicista* and *Cricetulus*) taken from Wahlert et al. (1993) in a parsimony analysis, conducted in PAUP* 4.0a167 (Swofford, 2003). The most parsimonious tree was compared with the cladogram presented in Wahlert et al. (1993), as well as with phylogenies of the Gliridae derived from molecular data (Montgelard et al. 2003; Nunome et al. 2007).

Results

Specimen descriptions

The reconstruction of Specimen 32206 is shown in Fig. 2. The skull includes one incisor and three molars on each side. The right pterygoid flange is broken, as is the ventralmost area of the right auditory bulla. The right orbitosphenoid appears to be displaced. The right occipital

area is slightly broken, showing small perforations of the skull. The ventralmost part of the left auditory bulla is slightly dented. The dentaries are fused at the mandibular symphysis and both have their full dentition intact: an incisor and three molars. The angular process of the right dentary is slightly broken but otherwise intact. The left coronoid process is broken and the most lateral tip of the left angular process is absent. No other features appear to be broken or deformed in the remainder of the mandible.

The reconstruction of Specimen S-28487 is shown in Fig. 2. The skull is not deformed, although it lacks multiple distinctive cranial features. Both upper incisors appear to have been cut and M1 and M2 are missing in the right molar row. Both zygomatic arches are missing and the auditory bullae are either broken or possibly sawn open. Some of the inner and middle ear morphology is therefore absent. The basioccipital area is broken posteriorly, as is part of the right occipital condyle. The part of the frontal bone located directly behind the zygomatic plate is broken on the right side, as is a part of the hard palate on the same side. The superior part of the infraorbital foramen on the left side is damaged when examined anteriorly. The mandible of this specimen is not fused at the symphysis, resulting in two separated dentaries. In the right dentary, the third molar is absent, the incisor alveolus is slightly broken laterally, and the tip of the coronoid process is missing, as is the middle and upper part of the angular process. All three molars are present in the left dentary. In addition, the incisor alveolus is very slightly broken ventrally, and the coronoid and angular processes are broken in a similar fashion to the right dentary of this individual.

Anatomical description

Numbers in square brackets correspond to the character list set out in the appendix of Wahlert et al. (1993). A full scoring of these characters in *Selevinia betpakdalaensis* alongside the character states for other dormice genera and four rodent outgroups from Wahlert et al. (1993) is given in ESM 3.

Cranium

In order to facilitate comparison, the skull shape of various dormouse genera are presented in Figs. 3-6. *Selevinia betpakdalaensis* is a small dormouse species, with the two specimens analysed for this study having skull lengths of roughly 21 and 24 mm compared with a range of 18 to 40 mm in other species (Holden-Musser et al. 2016). When examined dorsally, the posterior extent of the premaxilla is roughly at the same location as that of the nasal bones [1] and extends farther than the maxilla [2]. As in all other dormice genera, the anterior end of the premaxilla is tall and high above the most anterior part of the incisor alveolus [3]. The nasal bone varies significantly between both skulls. Specimen S-28487 has a much broader anterior part of the nasal bone in comparison with Specimen 32206. It is possible that this feature is deformed in the former specimen, but it is difficult to determine if this happened post-mortem or not. Nonetheless, both specimens indicate that the nasal bone is rather wide in comparison with most dormice genera. The infraorbital foramen is similar in size and position to in *Myomimus*, although *Myomimus* has more developed ridges on the lateral side of this foramen and flares more strongly inferiorly, resulting in a very pronounced anterior extension of the ventral margin. This extension is present, although less pronounced, in *Selevinia*. As *Selevinia* has a clearly reduced molar row, the diastema is technically longer than is seen in other dormice; however, there is a clear distinction between the area created by molar reduction and the area representing the diastemal palate in other genera. We will use the latter area for

assigning the diastema. This area appears to be very flat within *Selevinia* [4]. A tubercle defines the position of the origin of the superficial masseter [5], in contrast to *Graphiurus*, *Muscardinus* and *Glis*, in which the area is not always clearly separated by a tubercle. The zygomatic plate is of similar thickness to *Muscardinus,* but positioned more inferiorly compared to this genus and tilted more anteriorly. The presumed extension of the lateral masseter on to the zygomatic plate on the rostrum is present in this genus, similar to most dormouse genera (except *Graphiurus*) [6], and the medial masseter extends through the enlarged infraorbital foramen [7], similar to all other dormice. The combined extension of both the lateral and medial masseter on to the rostrum is characterised as the myomorphous condition.

The posterior edge of the anterior root of the zygoma is located anterior to the first cheek tooth [8]. This characteristic is also present in *Graphiurus*, whereas in all other genera it is lateral to the first premolar. The lack of premolars in *Selevinia* is unique within extant dormice and could well be impacting this characteristic. The lacrimal bone does not appear to be present in either of the two *Selevinia* specimens, although the scarcity of crania available to us makes it impossible to rule out the absence of this bone in all members of this genus. The lacrimal bone appears to be often broken or missing in dormice skulls, as it is often not completely fused with the cranium. In *Selevinia*, the jugo-maxillary suture is positioned posteriorly along the zygomatic arch to such an extent, that it seems very unlikely that any potential lacrimal bone would contact the jugal [9]. The zygomatic arches flare dorsally midway along the arch (forming a small postorbital process) and are similar in shape to *Muscardinus*, although the flaring occurs more posteriorly in *Selevinia.* The zygomatic arches are only slightly wider than the posterior part of the cranium, a trait not seen in other dormouse species. This results in a narrowing of the overall skull width.

On the ventral aspect of the skull, the premaxillary-maxillary suture connects with the incisive foramina near their midpoints [10], in a similar fashion to all other genera. The area between the anterior part of the incisive foramen and the incisor is of similar length to that of *Myomimus* and shorter than *Glis.* The ratio of incisive foramen length to diastema is roughly 85% [11] and therefore most similar to *Myomimus*. However, when using the full diastemal length (anterior part molar row to posterior part of the incisor alveolus), the ratio is only 69% and falls within the range of *Eliomys*. The anteromedial position of the palatine bone with respect to the molar row is located between the posterior part of M2 and the M2-M3 junction [12], relatively caudal compared to all other genera. This is thought to be a by-product of the reduction of the molar row. Furthermore, the reduction in molar size results in a relatively large palatal width between the M1 teeth in *Selevinia*, with a ratio of palatal width to condylobasilar length of 0.16 [13]. This ratio is also similar in many *Dryomys* and *Glirulus* specimens, but smaller in other genera. The posterior palatine foramen is within the palatine bone and medial to the M3 [14], similar to *Glirulus, Myomimus* and some *Graphiurus.* The posteriorly orientated spine on the medial posterior end of the palate is absent in *Selevinia* [15], whereas it is very weakly present in *Myomimus* and *Glis.* The opening of the posterior maxillary notch or foramen is a difficult characteristic to determine. Wahlert et al. (1993) distinguish various options within species for *Glis* and *Dryomys*, in which the notch or foramen is either well enclosed or just enclosed. We examined multiple species ourselves in order to correctly assign this character to *Selevinia* and noticed that our *Glirulus* specimen has no maxillary notch or foramen. Instead a foramen is present within the alisphenoid, which is well enclosed and could easily be confused with a maxillary foramen. Wahlert et al. (1993) originally assigned the well enclosed option for the maxillary foramen for *Glirulus*, but it is unclear from their figures whether this is because of an

incorrect identification of the alisphenoid canal or because of intraspecific variation within this species. *Selevinia* shows a maxillary notch rather than a foramen, which can be considered either just enclosed, or well enclosed. It appears to be more enclosed than our *Graphiurus* specimen, in which the maxillary notch is assigned just enclosed according to Wahlert et al. (1993). Following this reasoning, the characteristic of the enclosure of the maxillary notch in *Selivinia* is determined to be well enclosed [16].

Similar to all other dormice, the entrance of the lacrimal canal is situated anteromedially with respect to the infraorbital foramen [17]. The anterior part of the sphenopalatine foramen is slightly posterior to the middle of M2 [18], similar to *Glirulus* and *Myomimus* as well as some *Graphiurus* and *Dryomys* specimens. The non-ossification between the orbitosphenoid and the frontal is present within one of our *Selevinia* specimens, but absent in the other [19]. Where present it appears to have incorporated the ethmoid foramen. The anterior part of this area is dorsal to M3 and extends posterodorsally beyond M3. In the specimen lacking the non-ossification, the ethmoid foramen is more clearly identifiable and dorsal to M3 [20]. The optic foramen is located even more posteriorly [21] and is quite small [22], similar to *Myomimus* and *Glirulus*. The dorsal palatine foramen is positioned entirely posterodorsally to M3 [23] and relatively close to the sphenopalatine foramen [24] in comparison to *Eliomys* and *Dryomys*. The sphenofrontal foramen appears to be present in *Selevinia* [25], but the frontal bone does not extend all the way to this foramen [26]. There is no connection between the parietal bone and the alisphenoid [27].

The foramen ovale is distant from the posterior entrance of the alisphenoid canal [28], in a similar fashion to *Eliomys.* An accessory foramen ovale appears to be absent [29], which

corresponds with all other dormice. There is a fenestra anterodorsal to the masticatory foramen [30], which is absent in some *Muscardinus* and *Eliomys* specimens, and in all *Glis* and *Glirulus* specimens. The lateral pterygoid flange very is weakly developed in *Selevinia* [31] as opposed to *Glis glis*. Wahlert et al. (1993) indicate this pterygoid flange to be present also within *Muscardinus*, whereas it is clearly absent in our specimen of this species. Similar to all other dormice genera, the sphenopalatine vacuity in *Selevinia* extends to the edge of the anterior alar fissure, but is not visible in the orbit [32] as in *Eliomys* and some *Dryomys* specimens. The ratio of the distance between the posterior edge of M3 and the anterior part of the foramen ovale to the condylobasilar length for *Selevinia* is between 0.12 and 0.14 [33]. This is similar to most dormice genera – only the genus *Muscardinus* appears to have a ratio smaller than 0.1. The stapedial artery and the foramen in which the stapedius muscle takes its origin are present within *Selevinia*. These features are similar in size compared to those in our *Myomimus* specimens and therefore considered small [34].

The posterior part of the zygomatic arch is orientated relatively inferiorly with the most lateral part not extended posteriorly, as is seen in *Myomimus*, for example. The area bounded by the zygomatic arch is oblong in dorsal view, which is representative for smaller dormice species. Furthermore, the interparietal and parietal bones are curved, another feature often observed in smaller genera and juvenile dormice. A dorsal orbital ridge is quite strongly developed (compared to other dormouse genera) in both specimens. A groove potentially related to muscle attachment of the temporalis muscle is clearly visible on the squamosal when observed laterally. This groove is less apparent in *Muscardinus,* but much more pronounced in *Myomimus*. *Selevinia* and all other dormice genera have the postglenoid foramen positioned between the auditory bulla and the squamosal bone [35]. The posterior part of the squamosal

bone is solid [36], similar to *Glirulus*, *Glis*, *Graphiurus* and *Muscardinus*. No clear temporal foramen is present at the squamosal-parietal suture [37], and neither is this foramen present in any other genus.

The foramen magnum, although incomplete in S-28487, appears to be relatively enlarged. The foramen magnum is orientated caudally in a similar fashion to *Myomimus.* The auditory bullae in are greatly inflated in all dormice genera but *Glis*, in which this feature is only slightly inflated. *Selevinia* however shows exceptionally well-inflated auditory bullae [38], resulting in the length of this feature representing 36% and 37% of the total skull length respectively, significantly larger than in any other dormouse genus. Three primary septa appear to be present within the auditory bullae [39], similar to all other genera, with the exception of *Glirulus*.

Mandible

The mandibles of various dormouse genera are illustrated in Fig. 7. The mandibular material of *Selevinia* available for this study is slightly broken. However, most features are present and intact in Specimen 32206. The diastema is rather flat when considering other genera. The mandible of *Selevinia* is quite distinctive compared to other dormice, characterised by robust incisors, a lack of premolars, extremely small molars and a condyle that is posteriorly extended with respect to the angular process. The angular processes in the two specimens observed here are perforated with a single, large fenestra [40] in a similar fashion to that often seen in *Myomimus, Muscardinus, Dryomys* and *Eliomys.* The flaring of the angular process is not very significant and the muscle attachment area relatively small. The condyle stretches out posteriorly and has a relatively small condylar head. The coronoid process is only intact in one dentary, and it flares posteriorly and slightly laterally, as is common in other dormice species.

The inclination of the leading edge of the coronoid relative to the occlusal plane is a relatively difficult character to evaluate, as this can be affected by the orientation in which the specimen is examined. However, the coronoid margin appears to be more horizontal than that of *Myomimus*, a genus Wahlert et al. (1993) described as being orientated at less than 60° to the occlusal plane. Measuring this angle with the dentary in as flat an orientation as possible indicates an angle of 45° [41]. The concealing of the molars by the coronoid process is also a difficult character to assess, as it is not clearly specified how the dentary should be positioned in order to establish a lateral view. This is of importance due to the three-dimensionality of this bone, however flat it might appear. We evaluated mandibles of various genera and positioned them laterally in such manner that our findings were similar to that of Wahlert et al. (1993). When positioning the *Selevinia* mandibles in a similar way, the coronoid either concealed the posterior part of the m3, or no molar at all [42]. The masseteric ridge protrudes clearly and the most anterior part of the masseteric fossa is ventral to the anterior margin of the first molar [43]. This is relatively similar to all other dormice, with the exception of *Glis*, in which the fossa is positioned slightly more posteriorly. The bone in the region caudal to the posterior part of the incisor alveolus is noticeably thin. Furthermore, a large number of openings are present on the ventral side of the mandible, exposing parts of the embedded enlarged incisor.

Dentition

The dental formula for the upper and lower jaws is 1/0/0/3 in *Selevinia*. The upper incisors are very unlike the incisors of other dormice except for *Chaetocauda*, owing to the deep groove running down the lateral side of the enamel surface. *Chaetocauda* is the only dormouse genus lacking in our comparative dataset; however, Wang (1985) describes a deep groove in the medial anterior surface of the upper incisors. This description of the upper incisors of

Chaetocauda corresponds with what is seen in *Selevinia*, although it should be noted that the pictures in Wang (1985) are not clear enough to compare this feature accurately with our *Selevinia* specimens. The segmented incisor shows that this groove is already apparent at the origin of the incisor, located medially to the zygomatic plate. The enamel is relatively thin and evenly spread throughout the anterior part of the incisor. In our evaluation of the enamel characteristic we presume the enamel cap to grade into the lateral surface [44]. The incisors are orientated downwards and ever so slightly posteriorly.

The curvature of the lower incisors is similar to other dormice species, with the incisor root located inferoposteriorly to the last molar. The lower incisors are very robust in comparison to any of the other dormice species, but lack the anterior groove characterising the upper incisors. However, the lower incisors show a ridge on their occlusal surface which is likely a result of wear from the grooved upper incisors.

The ratio of upper cheek teeth crown length to condylobasilar length is very small (less than 0.2) in *Selevinia* [45], as a result of the very small, brachydont molars characterising this genus. The genus is also the only one in which all upper and lower premolars appear to be absent [46,47], although both *Muscardinus* and *Myomimus* show reduced premolars, in contrast to other genera. In the adult *Selevinia* specimens studied here, small cavities can be seen located anterior to the first upper molar. As Bashanov (1951) observed two deciduous premolars in juvenile *Selevinia* specimens, the cavities in our specimens are therefore identified as (remnants of) the alveoli of the deciduous fourth premolars.

The upper molars are concave and very simplistic, lacking any clear dental patterns on the occlusal surface, which is considered to be weakly helical in shape [48] compared to other genera. The occlusal surface of the molar row consists solely of enamel, with no dentine visible externally. The M2 is the largest molar in both specimens, being slightly larger than M1. Both M1 and M2 include two lingual lobes, but this is less clearly expressed in M1. M3 lacks these lobes completely and is roughly half the size of M2. The simplified molars in *Selevinia* do not include any cusps, and the buccal ridge of the molars is not more pronounced than the lingual ridge [49]. No distinct accessory crests or cusps are present within any of the molars of *Selevinia.* The root morphology varies per molar (Fig. 8), with the M1 having three roots, with the palatal root being the longest and the only one including a canal. The M2 also includes three roots, with the palatal root being the most developed. The anterior accessory root here fuses with the palatal root in both our specimens. The posterior accessory root appears to be shorter in M2 in comparison to M1 and flares more posteriorly. One canal is present within the M2, located in the palatal root. M3 is much more simplistic in comparison with the other molars in the molar row, including only a single canalized root. None of the other molar characteristics [50-54] is identifiable in *Selevinia* due to the reduced state of these teeth.

The lower molars are similar to those in the upper jaw, being concave, reduced in size and relatively simplistic in morphology. The relative molar sizes are similar as well, with m2 being the largest of the three molars and m3 clearly the smallest. No room for a premolar appears to be present within this species. Interestingly, the occlusal surface of the lower molar row appears to be larger than that of the upper molar row. Root morphology is more simplistic in the lower molar row, with all molars having one well developed root. m1 and m2 show

indications of a large posterior root fused with an anterior accessory root. Only one canal is present in every molar, similar to the upper molars.

Phylogenetic analysis The most parsimonious tree of dormouse genera based on cranio-mandibular and dental characters had a length of 150 and is given in Fig. 9. *Selevinia* is found to be most similar to *Myomimus*, and then to a grouping of *Eliomys* and *Dryomys*. These four genera are then most closely related to *Graphiurus*, with *Glis*, *Muscardinus* and *Glirulus* forming a separate group. Tree support values were CI = 0.613, RI = 0.536 and RC = 0.329.

Discussion

A number of unusual and highly derived morphological features within the skull and lower jaw of *Selevinia betpakdalaensis* were described using the virtual reconstruction of two specimens. The most obvious of these are the extremely reduced and simplified cheek teeth. Loss of the premolars is not unusual within rodents, occurring widely throughout the order, notably in the Muridae (although not in any other dormouse species). However, a reduction in the size and complexity of the molars is much less common, with the only other known examples of this phenomenon in rodents being specialist worm-eating taxa from Southeast Asia, such as *Paucidentomys*, *Pseudohydromys* and *Rhynchomys* (Esselstyn et al. 2012; Charles et al. 2013). Such a vermivorous diet is unlikely in *Selevinia* given the lack of an elongated rostrum and the presence of robust incisors, although it should be noted that the precise diet of this species is at the moment unclear. Captive specimens of this species were observed to consume mostly insects (Ognev, 1947), but an analysis of stomach contents of a wild specimen revealed undigested leaves of a desert plant, *Salsola laricifolia* (Bashanov and Belosludov, 1941). An insectivorous diet is most likely given the small, simple molars, but the robust incisors have

also been suggested as an adaptation to cropping tough vegetation (Holden-Musser et al. 2016).

The upper incisors of *Selevinia* are also highly unusual, displaying a prominent groove antero-laterally, which gives them an irregular cross-section. Analogues for this morphology seem to be present in some other rodents (Ohazama et al. 2010), such as the meadow jumping mouse (*Zapus hudsonius*) and the capybara (*Hydrochoerus hydrochaeris*), as well as being found in lagomorphs including pikas (Ochotonidae). It is unclear at the moment what advantage such a groove may convey.

The auditory bullae of most dormouse species are enlarged (Wahlert et al. 1993), but this trait is taken to the extreme in *Selevinia*, which has the largest bullae relative to cranial length of all Gliridae. This is perhaps not surprising as hypertrophied auditory bullae are known to be common in small desert mammals (Alhajeri et al. 2015; Mason, 2016). Such morphology increases the acuity of low frequency hearing and has the potential advantages to desert dwelling species of improving communication over long distances or better seismic detection. Enlarged auditory bullae are also common in fossorial rodents owing to the slower attenuation of low frequency sounds in subterranean tunnels (Schleich and Vassallo, 2003). Thus, it is possible that *Selevinia* is spending at least part of its life underground. This interpretation is also supported by other characters such as the relatively narrow width of the cranium, with the zygomatic arches being only slightly more laterally extended than the posterior part of the skull, and the caudal orientation of the foramen magnum. The latter character indicates a rectilineal posture, similar to *Myomimus*, which would be advantageous for moving through

underground tunnels. Considering the barren landscape of the Betpak-Dala Desert and the hibernating characteristics within most dormice, adaptations to burrowing would not be surprising in the desert dormouse.

The parsimony analysis of dormouse genera and four rodent outgroups produced a shortest tree very similar to that presented in Wahlert et al. (1993). The only difference was in the placement of *Graphiurus*, which was found to be the sister-group to all other dormouse genera in Wahlert et al. (1993), but was recovered as the sister-group to the Leithiinae (minus *Muscardinus*) in our analysis (Fig. 9). Although Wahlert et al. (1993) did not formally include *Selevinia* in their cladistic analysis, they hypothesised that it would be the sister-genus to *Myomimus*, and this is what we found here. More recent molecular phylogenies of the Gliridae (Montgelard et al. 2003; Nunome et al. 2007) show roughly similar topologies to that recovered here, but differ in the placement of *Muscardinus* which is found to be the sister-genus to the Leithiinae, and not closely related to *Glis* and *Glirulus*. This has led to the inclusion of *Muscardinus* within Leithiinae in recent classifications (Wilson & Reeder, 2005; Holden-Musser et al. 2016). There is also continued uncertainty in the position of *Graphiurus*, with Montgelard et al. (2003) placing it as the first branching genus (as also seen in Wahlert et al. 1993), but Nunome et al. (2007) finding it to be sister-group to the Leithiinae, thus agreeing more closely with the analysis presented here. At the time of writing, *Selevinia* has yet to be included in a molecular-based phylogenetic analysis of dormice.

As noted above, the reduced state of the molars in *Selevinia* prevents accurate coding of characters 50-54 (they were scored as missing in the parsimony analysis conducted here). Thus, these are excluded in all further discussion, leaving a total of 49 characters. When

compared with the taxa analysed by Wahlert et al. (1993), *Selevinia* appears to resemble the small dormouse genus *Myomimus* most closely, sharing 39 of the 49 characters (Table 1). *Dryomys* follows *Myomimus* with 36 corresponding characters, closely followed by *Graphiurus* (35). Interestingly, the genus *Muscardinus* does not seem to resemble *Selevinia* greatly (23 shared characters) despite being similar in cranial size, i.e. very small for dormice. Notwithstanding some controversy over the phylogenetic position of *Muscardinus* (Wahlert et al. 1993; Montgelard et al. 2003; Nunome et al. 2007) it is clear that this genus is not particularly closely related to *Selevinia*. This evolutionary distance may have led to the morphological differences between the genera. Alternatively, strong functional adaptation of the teeth (relatively large and densely ridged molars in *Muscardinus*, and simplified and reduced molars in *Selevinia*) may have driven a divergence in overall cranial morphology. Both *Myomimus* and *Muscardinus* are characterised by a size reduction of the premolars. We hypothesise that *Selevinia* went through a similar premolar size reduction phase before losing its premolars completely.

The similarity of *Selevinia* to *Myomimus* was expected and predicted by Wahlert et al. (1993). Furthermore, the similarity to *Dryomys* is understandable, as *Myomimus* has previously been proposed as a subgenus of *Dryomys*. However, the number of shared characteristics with *Graphiurus* was surprising, as *Muscardinus* is phylogenetically closer to *Myomimus* and *Dryomys* than to *Graphiurus* (Montgelard et al. 2003). Initially we hypothesised that the broad range of *Graphiurus* species may have resulted in many variable characters to be present within the genus, explaining the large potential correlation with *Selevinia*. However, when analysing the number of characters that are polymorphic within *Graphiurus,* we did not find an exceptionally large number (4 out of 49), especially when compared with *Dryomys* (8 out of

49). Potentially, some primitive cranial characteristics are present in both the sub-Saharan dormice and the desert dormouse. It would be extremely interesting to include *Selevinia* in a phylogenetic study, in order to know the placement of this peculiar species within Gliridae.

Our analysis of the cranial and mandibular morphology of the desert dormouse, *Selevinia betpakdalaensis*, shows that this species is morphologically very similar to the mouse-tailed dormice in the genus *Myomimus.* Derived cranial features are suggested to be adaptations to a burrowing lifestyle in a desert environment; these include extremely enlarged auditory bullae, and a reduced molar row both in number and size of teeth, as well as a less lateral extension of the zygomatic arch, relative to the posterior part of the skull. The detailed description of the cranial morphology will facilitate more reliable comparisons of *Selevinia* with other dormice, leading to a more complete overview of cranial and mandibular shape variation within the rodent family Gliridae.

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Author contributions

JJH and PGC conceived the study. JJH segmented the data and undertook the character analysis. JWFS produced the illustrations. FNG, LYK, DK, ON provided access to specimens. JJH and PGC drafted the manuscript. All authors contributed to the editing of the final manuscript and gave final approval before submission.

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Tables

Table 1: Number of shared characters between dormouse genera included by Wahlert et al. (1993) and the desert dormouse *Selevinia betpakdalaensis*.

Number of characters shared with *Selevinia*	Dormouse genus
39	*Myomimus*
36	*Dryomys*
35	*Graphiurus*
34	*Eliomys*
29	*Glirulus*
23	*Muscardinus*
21	*Glis*

Figure captions

Figure 1: Skin of *Selevinia betpakdalaensis,* specimen S-28487 (paratype), in (a) dorsal and (b) ventral view.

Figure 2: Virtual reconstructions of the cranium and mandible of *Selevinia betpakdalaensis* in left lateral view, (a) specimen 32206, (b) specimen S-28487. Note the characteristic grooved upper incisors, the robust lower incisors, reduced size of the molars and the greatly inflated auditory bullae.

Figure 3: Glirid skulls, right lateral view, zygomatic arch removed.

Abbreviations for foramina and other apertures: ac, alisphenoid canal, posterior end; bu, buccinator; dpl, dorsal palatine; eth, ethmoid; fo, foramen ovale; hy, hypoglossal; ifo, infraorbital; in, incisive; ito, interorbital; ju, jugular; mlf, middle lacerate; msc, masticatory; nl, nasolacrimal; op, optic; paf, posterior alar fissure; pgl, postglenoid; pom, posterior maxillary; ppl, posterior palatine; sf, sphenofrontal; spl, sphenopalatine; spv, sphenopalatine vacuity; stm, stapedius muscle canal; sty, stylomastoid; trc, transverse canal; un, unossified area.

Abbreviations for bones and their processes: as, alisphenoid; ab, auditory bulla; bo, basioccipital; bs, basisphenoid; f, frontal; ip, interparietal; j, jugal; 1, lacrimal; m, maxilla; mst, mastoid region; n, nasal; oc, occipital; os, orbitosphenoid; p, parietal; pl, palatine; pm, premaxilla; ps, presphenoid (continuous with orbitosphenoid); sq, squamosal.
This image is modified with permission from Wahlert et al. (1993) by the inclusion of the *Selevinia* skull.

Figure 4: Glirid skulls, ventral view. See Figure 3 for abbreviations. Image is modified with permission from Wahlert et al. (1993) by the inclusion of *Selevinia.*

Figure 5: Glirid skulls, dorsal view. See Figure 3 for abbreviations. Image is modified with permission from Wahlert et al. (1993) by the inclusion of *Selevinia.*

Figure 6: Glirid skulls, frontal view. See Figure 3 for abbreviations. Image is modified with permission from Wahlert et al. (1993) by the inclusion of *Selevinia.*

Figure 7: Glirid mandibles, right buccal views. Abbreviations: an, angle; con, condyloid process; cor, coronoid process; d, dentary bone; fen fenestra; mfos, masseteric fossa; mt, mental foramen; san, superior angular process. Image is modified with permission from Wahlert et al. (1993) by the inclusion of *Selevinia* and the coronoid process of *Glirulus.*

Figure 8: (a) Rendering of specimen 32206 with the dentition segmented separately showing the extent of the molar roots and the origin of the incisors. (b) Enlarged lateral (lingual) view of the upper and lower molar rows (left, mesial; right distal) in the original resolution (4.9 µm).

Figure 9: Most parsimonious tree recovered from analysis of 54 cranial, mandibular and dental characters. Character states for all taxa except *Selevinia* taken from Wahlert et al. (1993).

Figure 1

Figure 2

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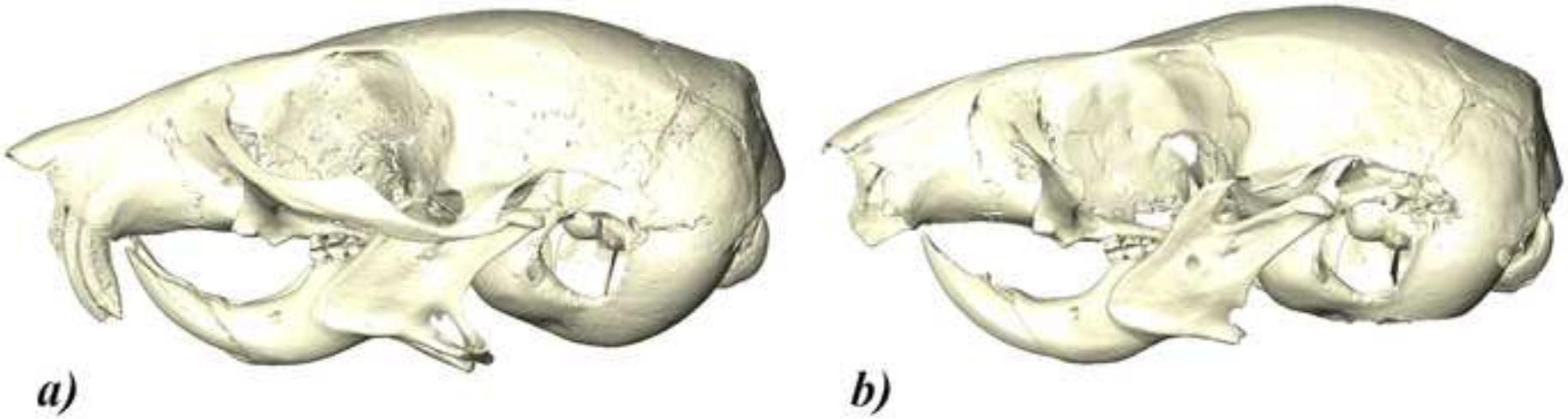

Figure 3

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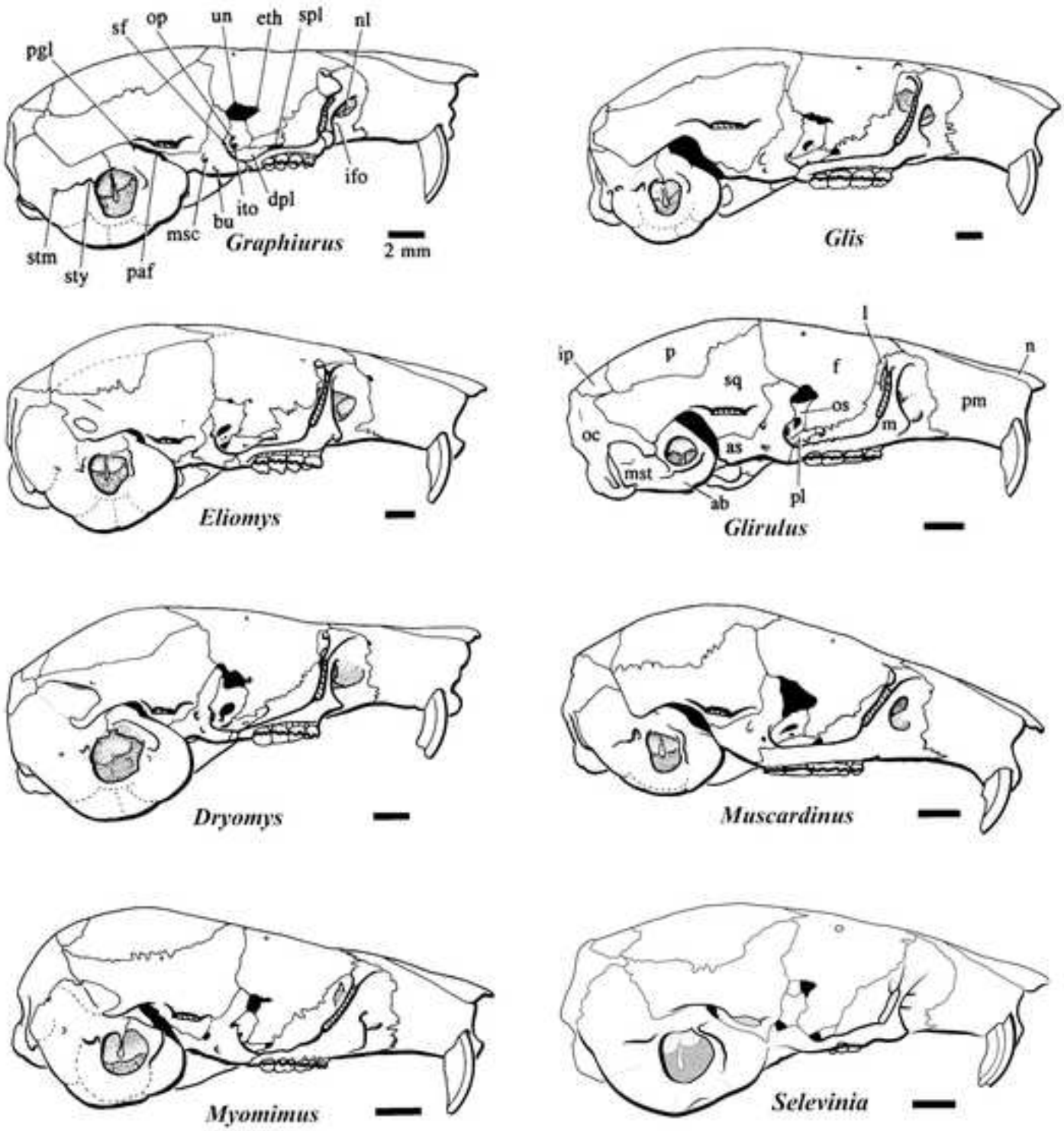

Figure 4

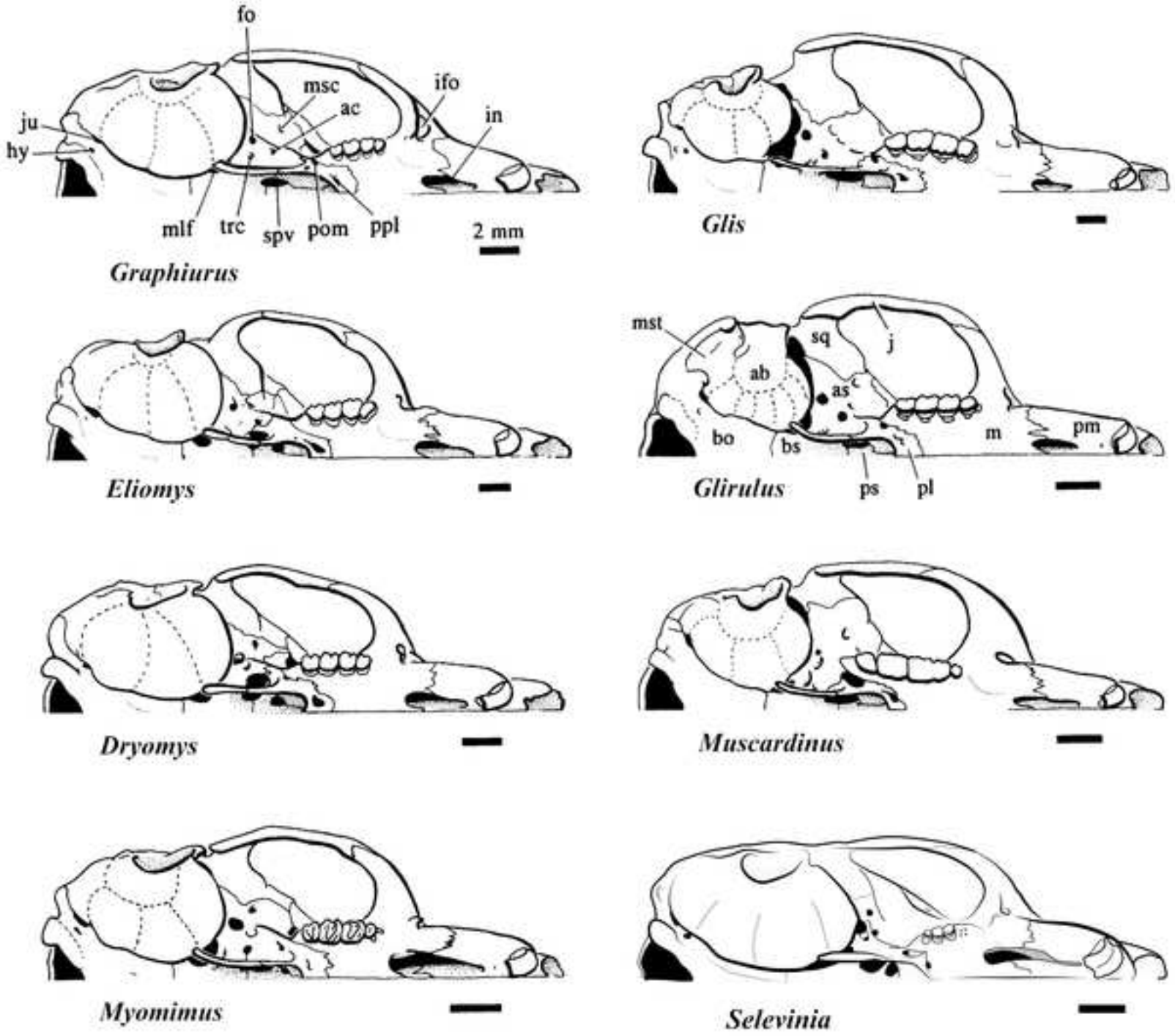

Figure 5

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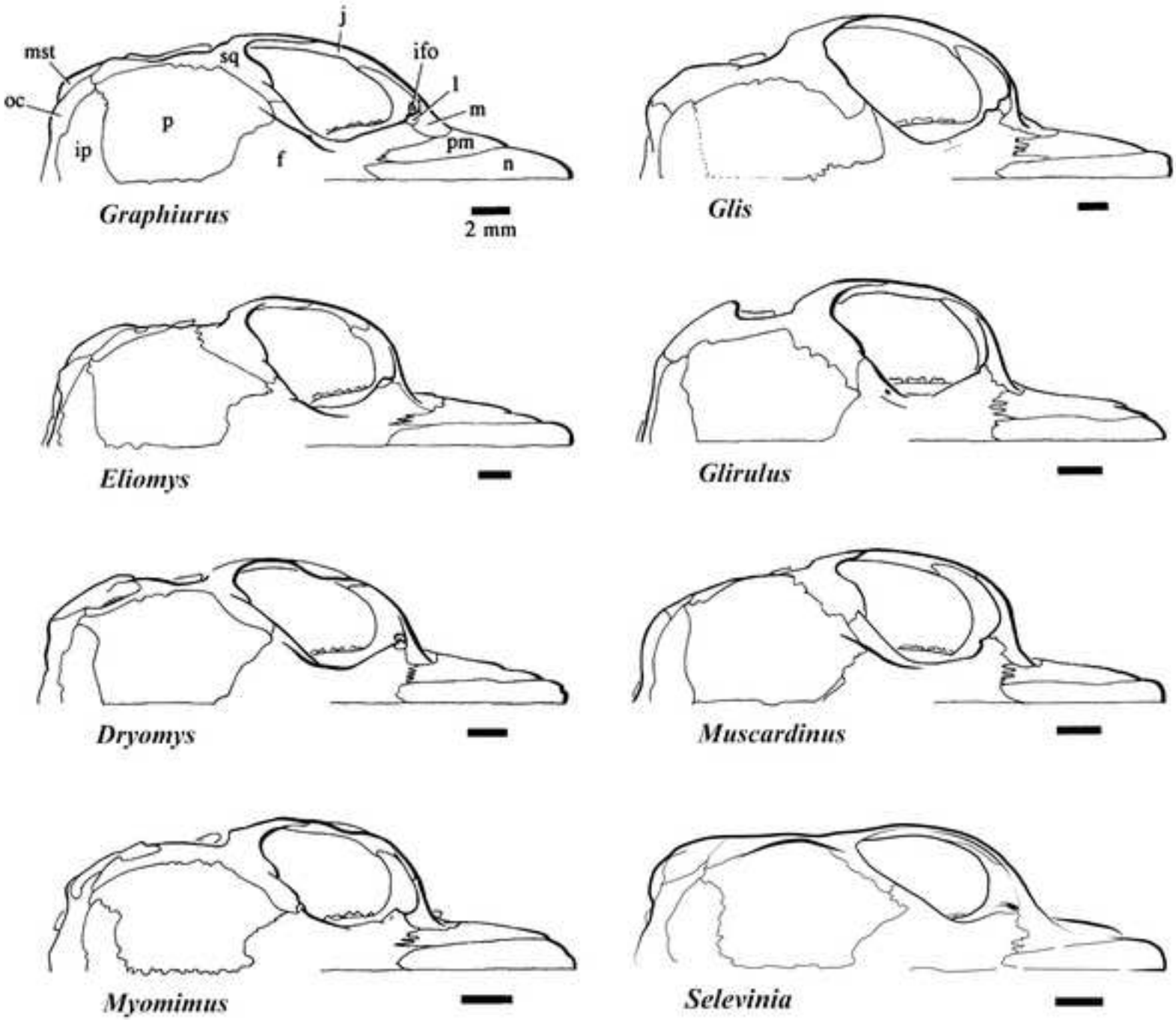

Figure 6

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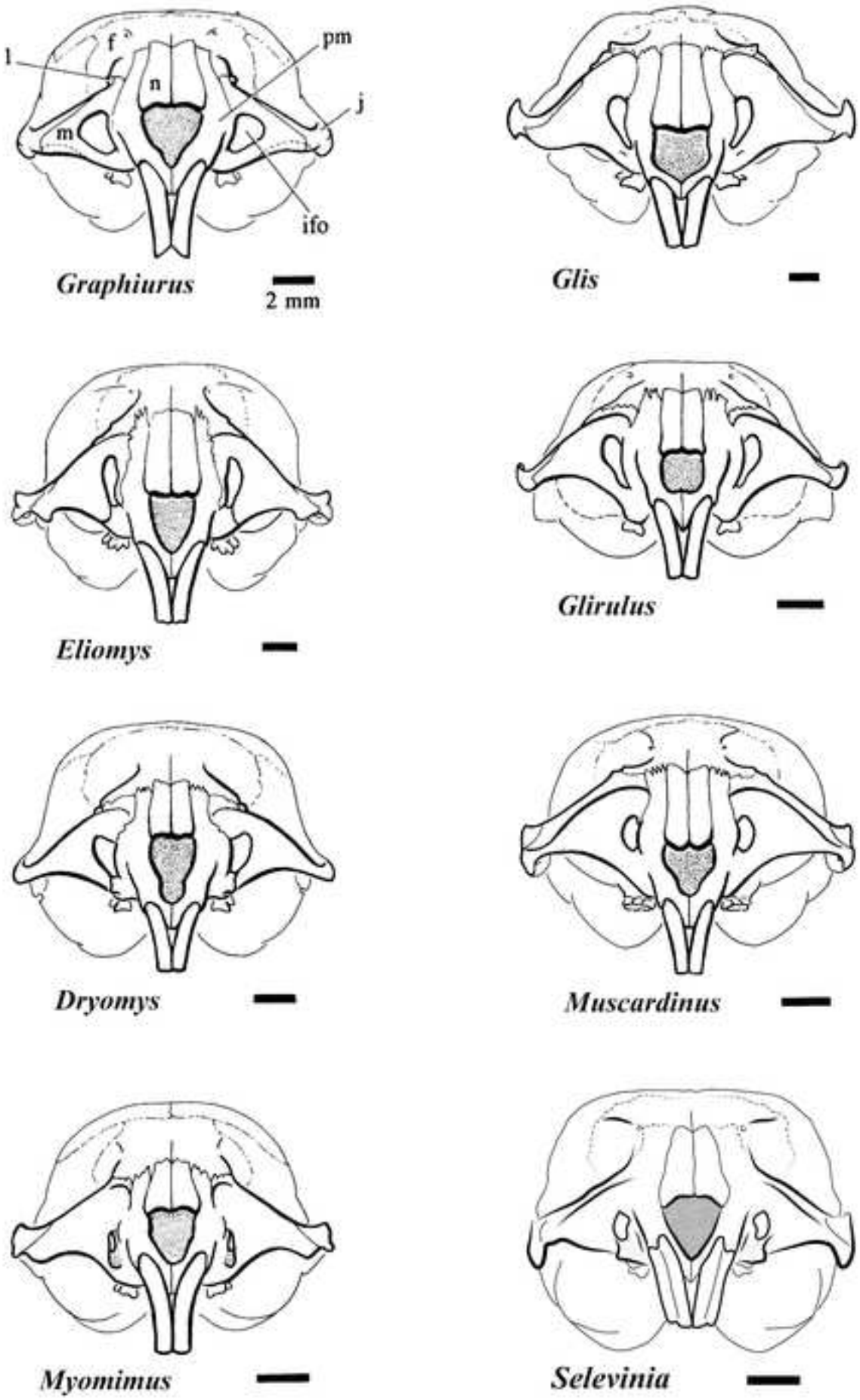

Figure 7

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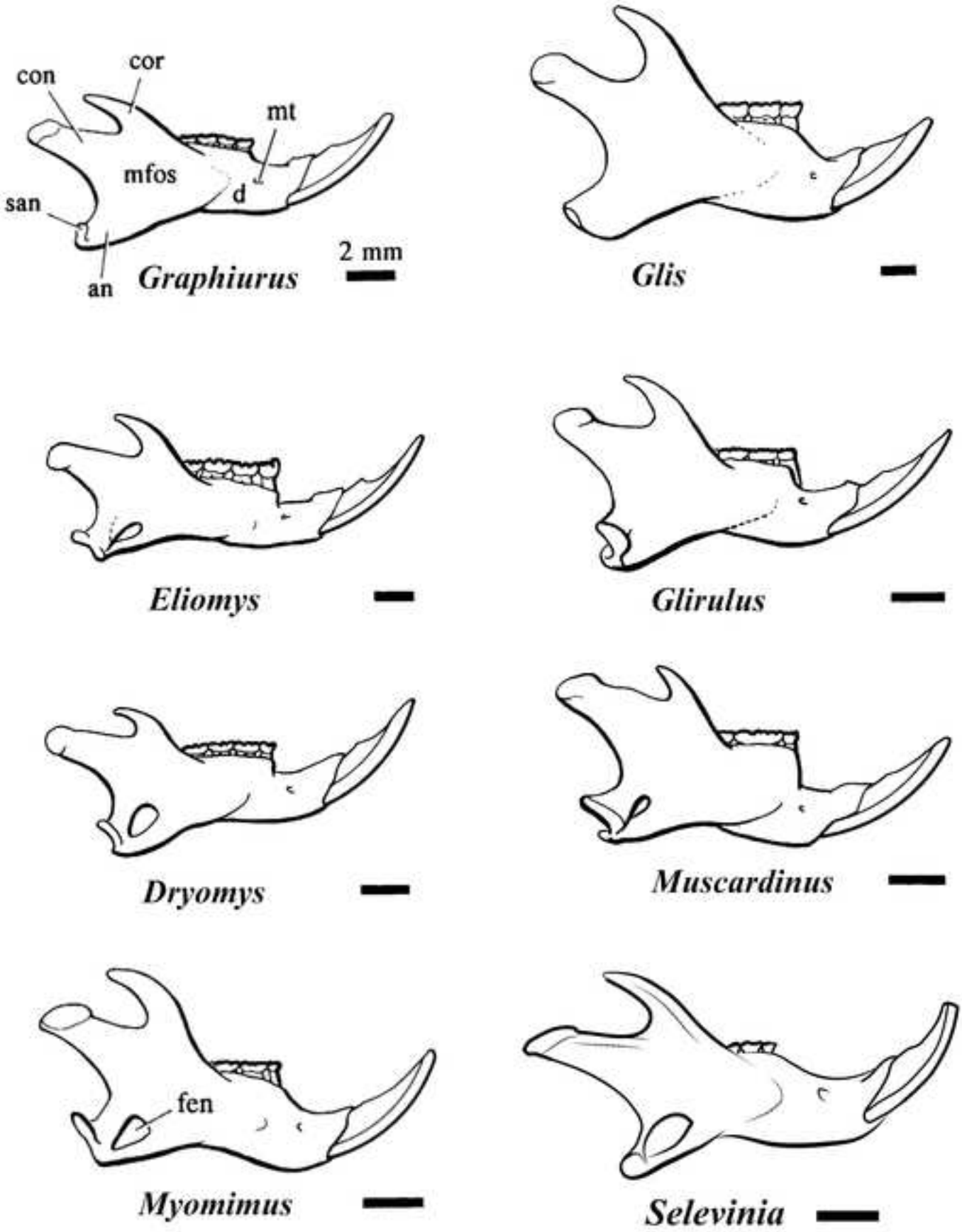

Figure 8

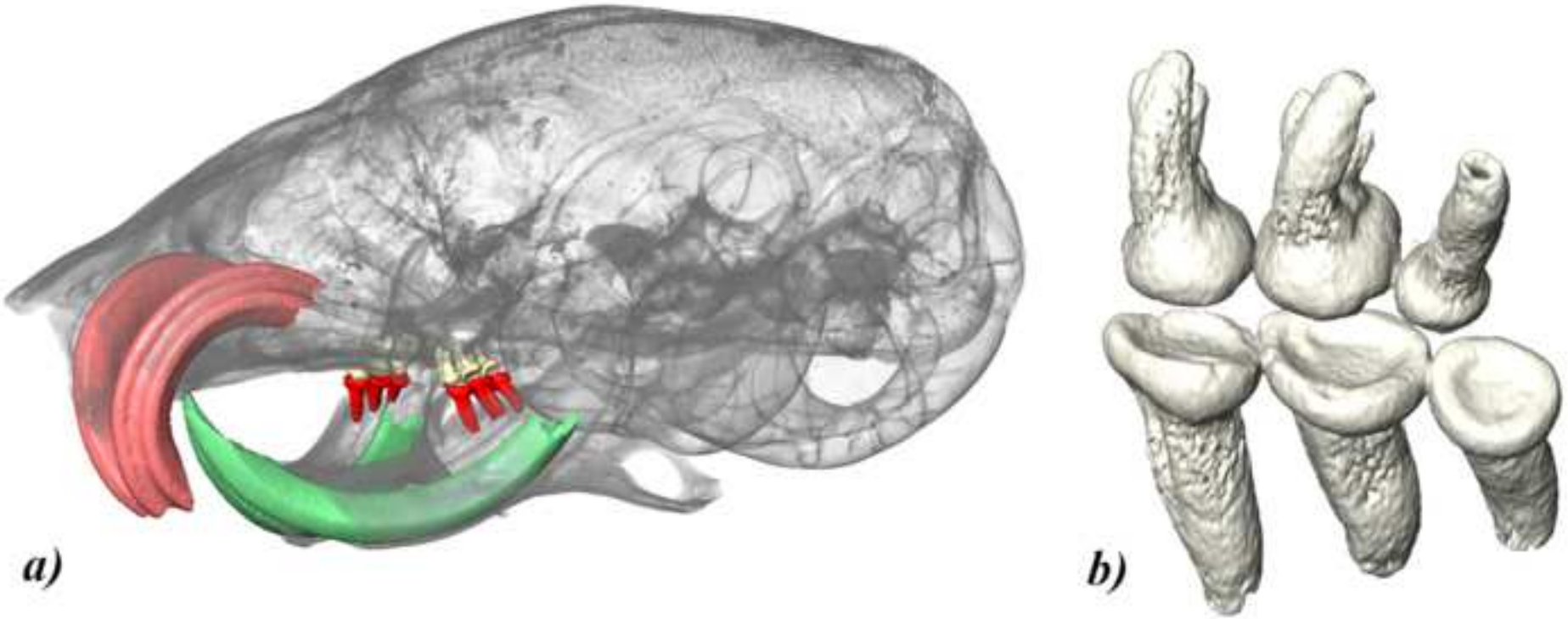

Figure 9

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